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Oceanographic drivers of marine mammal and seabird habitat-use across shelf-seas: A guide to key features and recommendations for future research and conservation management

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ABSTRACT

Mid-latitude (~30-60°) seasonally stratifying shelf-seas support a high abundance and diversity of marine predators such as marine mammals and seabirds. However, anthropogenic activities and climate change impacts are driving changes in the distributions and population dynamics of these animals, with negative consequences for ecosystem functioning. Across mid-latitude shelf-seas marine mammals and seabirds are known to forage across a number of oceanographic habitats that structure the spatio-temporal distributions of prey fields. Knowledge of these and the bio-physical mechanisms driving such associations are needed to improve marine management and policy. Here, we provide a concise and easily accessible guide for both researchers and managers of marine systems on the predominant oceanographic habitats that are favoured for foraging by marine mammals and seabirds across mid-latitude shelf-seas. We (1) identify and describe key discrete physical features present across the continental shelf, working inshore from the shelf-edge to the shore line, (2) provide an overview of findings relating to associations between these habitats and marine mammals and seabirds, (3) identify areas for future research and (4) discuss the relevance of such information to conservation management. We show that oceanographic features preferentially foraged at by marine mammals and seabirds include shelf-edge fronts, upwelling and tidal-mixing fronts, offshore banks and internal waves, regions of stratification, and topographically complex coastal areas subject to strong tidal flow. Whilst associations were variable across taxa and through space and time, in the majority of cases interactions between bathymetry and tidal currents appear to play a dominant role, alongside patterns in seasonal stratification and shelf-edge upwelling. We suggest that the ecological significance of these bio-physical structures stems from a capacity to alter the densities, distributions (both horizontally and vertically) and/or behaviours of prey in a persistent and/or predictable manner that increases accessibility for predators, and likely enhances foraging efficiency. Future conservation management should aim to preserve and protect these habitats. This will require adaptive and holistic strategies that are specifically tailored to the characteristics of an oceanographic feature, and where necessary, evolve through space and time in response to spatio-temporal variability. Improved monitoring of animal movements and bio-physical conditions across shelf-seas would aid in this. Areas for future research include multi-disciplinary/trophic studies of the mechanisms linking bio-physical processes, prey and marine mammals and seabirds (which may elucidate the importance of lesser studied features such as bottom fronts and Langmuir circulation cells), alongside a better understanding of how predators perceive their environment and develop foraging strategies during immature/juvenile stages. Estimates of the importance of oceanographic habitat features at a population level should also be obtained. Such information is vital to ensuring the future health of these complex ecosystems, and can be used to assess how anthropogenic activities and future environmental changes will impact the functioning and spatio-temporal dynamics of these bio-physical features and their use by marine predators.

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1. Introduction

Mid-latitude (~30-60°) seasonally stratifying shelf seas cover less than 8% of the world's oceans, yet account for ~15% of marine global productivity (Muller-Karger et al., 2005; Simpson and Sharples, 2012). These regions support high abundances of species above the base of the food web, which includes a diversity of marine predators such as marine mammals and seabirds. However, they are currently going through a period of rapid alteration, driven by the combined and cumulative effects of a range of anthropogenic activities and impacts such as climate change, fisheries and the development of marine renewables (Walther et al., 2002; Frid et al., 2005; Witt et al., 2012; Avila et al., 2018; Kroodsma et al., 2018). As a result, many populations of marine mammals and seabirds in shelf-seas have shifted in distribution (Bertrand et al., 2012; Hazen et al., 2013) or suffered severe declines (Cury et al., 2011; McCauley et al., 2015; Paleczny et al., 2015), which has negatively impacted the functioning of these systems as a whole (Heithaus et al., 2008). Addressing this issue represents a major environmental conservation challenge, requiring response at the policy level alongside informed management practices.

Marine mammals and seabirds meet their requirements for survival, growth and reproduction through the exploitation of prey resources from their surrounding environment. Whilst typically these animals are highly mobile and capable of ranging vast distances (Block et al., 2011), foraging efforts are often concentrated over localised spatio-temporal scales (Hastie et al., 2004; Sydeman et al., 2006; Weimerskirch, 2007). Such heterogeneity in distributions is expected to match the organisation of prey, but this has proved surprisingly challenging to demonstrate (Logerwell et al., 1998; Fauchald and Erikstad, 2002; Gremillet et al., 2008; Torres et al., 2008), particularly at finer scales which may be impacted by confounding factors (Schneider and Piatt, 1986; Hunt et al., 1992; Mehlum et al., 1999; Swartzman and Hunt, 2000; Vlietstra, 2005; Fauchald, 2009). Increasing evidence suggests the behavioural patterns of marine predators (particularly those feeding on plankton and/or forage and pelagic fish) are linked to bio-physical oceanographic processes that structure the accessibility and availability of these lower trophic level food sources (Cox et al., 2013; Bertrand et al., 2014; Woodson and Litvin, 2015; McInnes et al., 2017), and thus influence foraging efficiency/success (Boyd et al., 2016). Across shelf-sea environments, a number of discrete habitat features have been identified as important locations that host enhanced foraging opportunities, including fronts, offshore banks where internal waves propagate and tidally dependent island wakes (Hunt and Schneider, 1987; Hunt et al., 1999; Bost et al., 2009; Bertrand et al., 2014; Scales et al., 2014a; Benjamins et al., 2015). Given the tight energy constraints of many marine mammals and seabirds (Cairns, 1988), these structures can be thought of as critical habitat features.

Knowledge of the bio-physical processes that underlie links between oceanographic habitat features and marine mammal and seabird foraging is vital to obtaining a comprehensive understanding of marine ecosystem functioning. This will prove invaluable as we move towards implementing holistic management methods, that consider ecosystems in their entirety and aim to incorporate more precautionary conservation measures (Arkema et al., 2006; Hooker et al., 2011). Early synthesises and reviews have outlined the prominent bio-physical processes occurring across ocean environments and how these are linked to the spatio-temporal distributions of seabirds (e.g. Hunt, 1990, 1991; 1997; Hunt et al., 1999), but no known equivalent review exists for marine mammals. Over the past 10–15 years, methodological and technological advances have substantially improved the way in which the marine environment is studied, both in terms of how we collect data (Cooke et al., 2004; Hunt and Wilson, 2012; Brown et al., 2013; Waggitt and Scott, 2014; Photopoulou et al., 2015; Benoit-Bird and Lawson, 2016; Macaulay et al., 2017) and quantitatively analyse it (Redfern et al., 2006; Wakefield et al., 2009; Brown et al., 2013; Carter et al., 2016; Bennison et al., 2017). As such, our knowledge of links between oceanographic habitats and marine predators has substantially improved, and a more mechanistic understanding of how these features aid marine mammal and seabird foraging, and function as dynamic habitats is being attained. Although, more recent regional and/or feature specific reviews have been published (e.g. fronts; Scales et al., 2014a, southern ocean fronts and eddies; Acha et al., 2004; Bost et al., 2009, and tidal stream environments; Benjamins et al., 2015), as of yet, a paper which encompasses links between both marine mammals and seabirds with the full range of oceanographic habitat features that occur across mid-latitude, seasonally stratifying shelf-seas as a whole is lacking. Such knowledge is still yet to be fully integrated into studies examining behavioural patterns and habitat use by marine predators alongside marine management strategies (Tremblay et al., 2009; Fourcade et al., 2018), and so it is particularly pertinent that this is addressed, not least because the diverse human use of shelf-seas is accelerating impacts on these ecosystems. We feel it important to synthesise the broad and diverse habitat features present in this environment to facilitate conservation management and ecological research, and drive a policy response to this crisis.

In light of this, we provide a concise and easily accessible guide for both researchers and managers of marine systems on the predominant oceanographic habitats that are favoured for foraging by marine mammals and seabirds across mid-latitude shelf-seas. We identify and describe key discrete physical features present across the continental shelf, working inshore from the shelf-edge to the shore line (Figs. 1 and 2, Table 1), and discuss links to marine mammals and seabirds. We then highlight the key characteristics of these structures that make them attractive as foraging habitats. We identify areas where knowledge is lacking and make recommendations for the direction of future research. Finally, we discuss how these insights can be used to improve the conservation management of shelf-sea environments. Our aim is to provide a concise overview, in a format that is broken down into feature specific sections accessible to non-oceanographers. In doing so we hope to encourage both researchers and conservation managers of marine systems to move towards the identification, bio-physical characterisation and incorporation of discrete oceanographic habitat structures that promote prey availability into future studies and management strategies.

2. The shelf edge

The shelf edge marks the transition zone from the comparatively shallow (usually less than 200 m) waters of the continental shelf to the deep abyssal plains (where depths exceed 2000m) of the open ocean (Simpson and Sharples, 2012). This region is relatively narrow, with a typical lateral distance of around 50 km, and so generally characterised by a steep sloping profile (e.g. the European continental shelf-edge). Along the shelf edge, dependent upon geographical location (e.g. bordering a major eastern boundary current), shelf-edge fronts and wind-driven upwelling fronts support high levels of primary and secondary productivity which attract a diversity of marine mammals and seabirds.

2.1. Shelf-edge fronts

Shelf-edge fronts (also shelf-break and shelf-slope fronts) occur at the interface between on-shelf and open-ocean waters (Fig. 1), and are marked by strong gradients in salinity, and sometimes temperature. As currents, pushed onto the shelf via tidal forcing, are interrupted by the steep sloping topographic profiles of these regions, upwelling pushes the surface mixed layer above the critical depth for phytoplankton growth (Fournier et al., 1979), whilst simultaneously facilitating exchange with the nutrient rich waters of the open-ocean's bottom boundary layer (Springer et al., 1996; Ryan et al., 1999). High levels of primary productivity are typically sustained, sometimes perennially (Fournier et al., 1979), attracting planktivorous grazers alongside large numbers of pelagic fish (Podesta et al., 1993; Sabatés and Olivar, 1996;

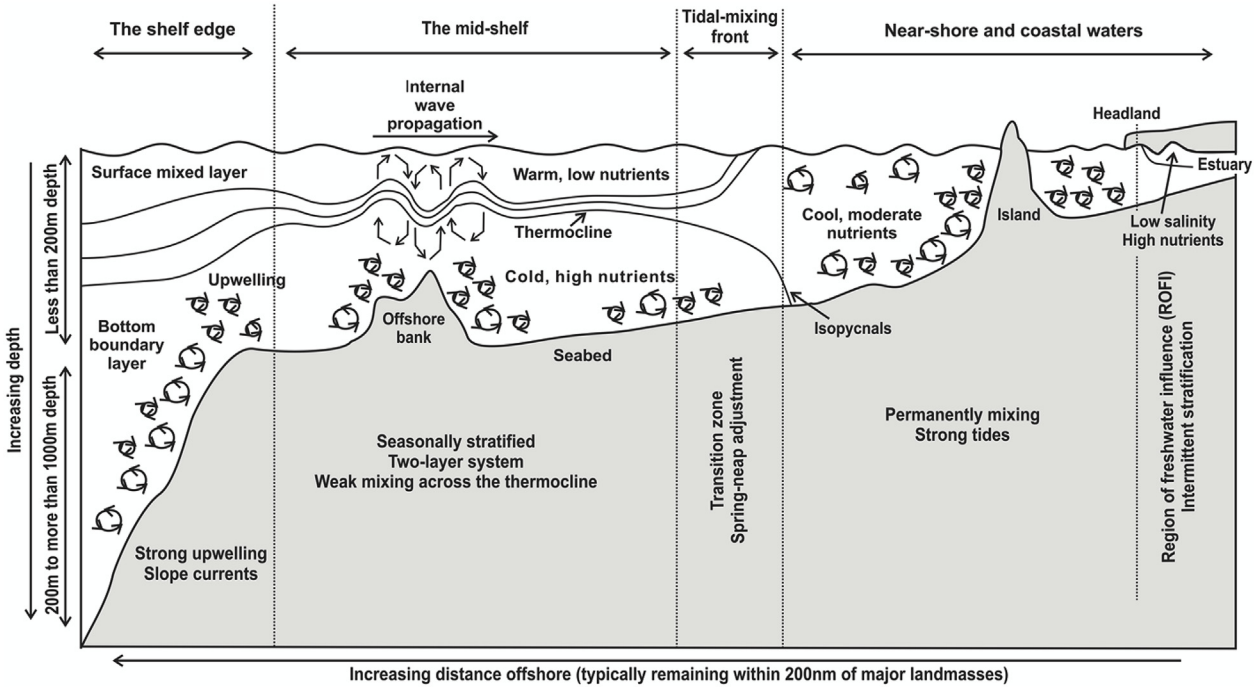

Fig. 1. Cross shelf schematic giving an overview of the typical oceanographic structure of thermally stratifed shelf-sea environments at mid-latitudes during the summer months. Adapted from Simpson and Sharples (2012), black directional arrows show (1) turbulent mixing around the seabed, offshore banks and islands (circular arrows), and (2) convergent and divergent upwelling and downwelling currents associated with the passage of internal waves (angled arrows).

Springer et al., 1996; Genin, 2004; Greer et al., 2015). Dependent upon the lateral extent and topography of the adjacent continental shelf, these features may be far from land, and so relatively inaccessible to those foragers constrained to land-based colonies (e.g. breeding seabirds and some seals). Links to marine predators are dominated by those taxa capable of performing far-ranging foraging trips (e.g. black petrel *Procellaria parkinsoni*, fork-tailed storm petrel *Oceanodroma furcate*, northern fulmar *Fulmarus glacialis*, short-tailed albatross *Phoebastria albatrus*; Schneider, 1982; Stone et al., 1995; Piatt et al., 2006; Freeman et al., 2010) or that are not restricted to a central location for breeding (e.g. Cuvier's beaked whale *Ziphius cavirostris*, Risso's dolphin *Grampus griseus*, sperm whale *Physeter microcephalus* and spotted

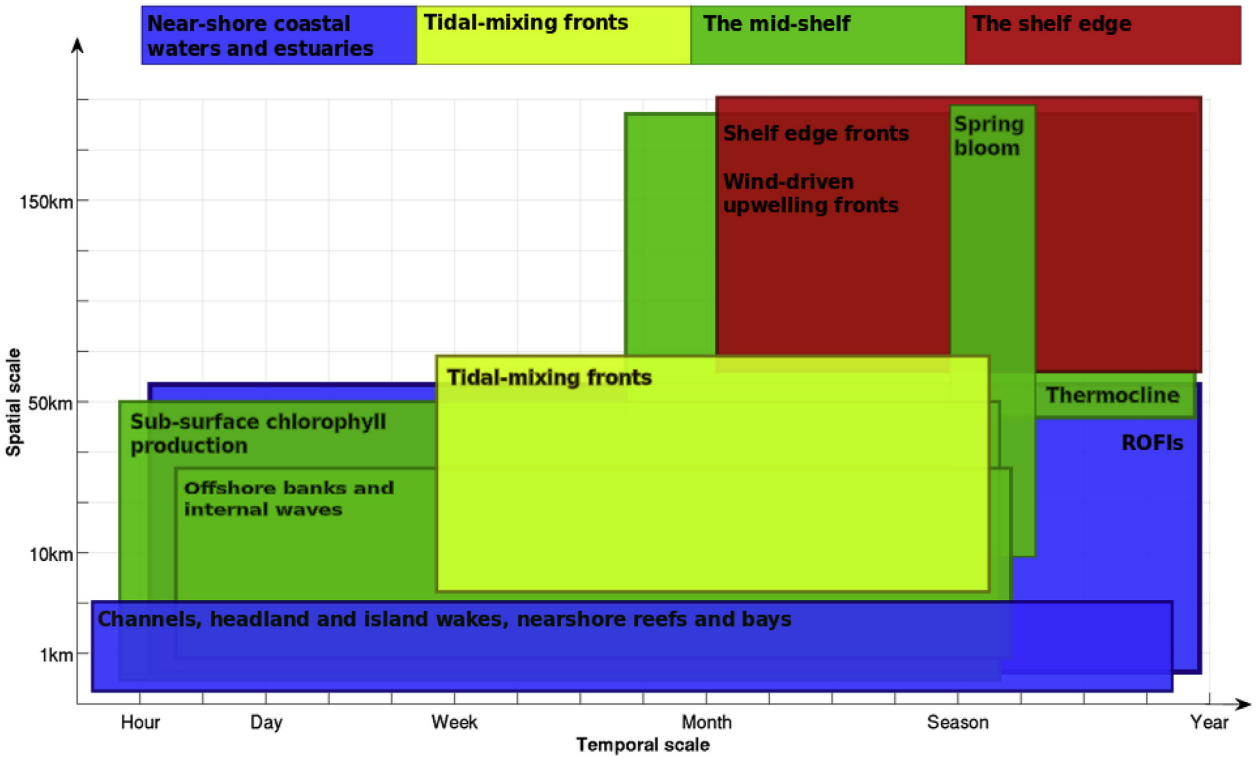

Fig. 2. Overview of the typical spatio-temporal scales oceanographic structures across shelf-sea environments function over. Further details can be found in Table 1.

Table 1
Details of the generalised spatio-temporal scales over which oceanographic features favoured for foraging across shelf-seas function. Columns from left to right list a features name, the spatial and temporal extent its expanse covers respectively, and finally the spatio-temporal scales over which variation may occur. References are provided for specific examples of features functioning in this manner. Note that regional and site specific differences in physical forcing mean there is variation around these generalisations in spatio-temporal scale, which should be assessed and considered.

BIO-PHYSICAL HABITAT FEATURE	SPATIAL EXTENT	TEMPORAL EXTENT	SPATIO-TEMPORAL VARIATION
Shelf-edge fronts	Lateral extent of 10's - ~100 km. Length may exceed 100's km's (e.g. Celtic shelf break and along the edge of the continental shelf of the Bering Sea; Pingree et al., 1981; Springer et al., 1996).	Typically persist perennially, although strength and associated productivity may vary seasonally (Fournier et al., 1979; Ryan et al., 1999).	Geographical location may shift 10's km's with prevailing meteorological conditions, seasonal changes and climatic fluctuations (Linder and Gawarkiewicz, 1998). Intensity may also vary over similar spatial scales (e.g. the strength of frontal interfaces as determined by horizontal gradients in sea surface temperature), and inter-annually with impacts on associated productivity (Fournier et al., 1979).
Wind-driven upwelling fronts	Lateral extent of 10's to ~100 km. Length may exceed 100's km's (e.g. along the California and Humbolt Currents; Acha et al., 2004; Letelier et al., 2009; Kahru et al., 2012).	Generally display some seasonality in occurrence in response to upwelling intensity with current flows and wind events (Kampf et al., 2004; Bograd et al., 2009b; Letelier et al., 2009).	Geographical location may shift 10–100's km's seasonally and inter-annually with climatic fluctuations in upwelling intensity, which may also impact frontal intensity and productivity levels (Bograd et al., 2009b; Letelier et al., 2009). Surface convergences and instabilities within these zones may be more ephemeral in occurrence, and linked to local meteorological conditions (Capet et al., 2008).
Spring bloom	Can extend across stratified section of the shelf-sea, encompassing areas exceeding 100's km^2 (e.g. Celtic & North Seas; Pingree et al., 1976; Holligan et al., 1989).	Seasonally occurring in spring for a period lasting no more than a month (typically around 1–2 weeks; Pingree et al., 1976; Townsend and Spinrad, 1986; Mills et al., 1994).	Initial date may vary with the spring-neap cycle alongside changes in climatic conditions (Hunt and Stabeno, 2002; Mann and Lazier, 2006; Sharples et al., 2006), which can also impact magnitude of productivity (Sambrotto et al., 1986). Regional variation in initial start date also occurs (e.g. latitudinally; Henson et al., 2009). Smaller scaled shifts in geographical occurrence may also occur inter-annually (e.g. across the Bering Sea; Hunt and Stabeno, 2002).
Vertical interfaces in stratified regions (i.e. the pycnocline)	Vertical extent of 10 cm's to a few metres (Simpson and Sharples, 2012). Horizontally extends across offshore stratified section of shelf-sea, which may encompass 100's km^2 (Pingree, 1975; Holligan et al., 1989).	In offshore waters may be persistent perennially, although depth and inshore extent varies seasonally, and is most prominent during spring, summer and early autumn (Pingree, 1975).	Inshore extent and depth can vary inter-annually, seasonally, and on short time-scales (days to weeks), with climatic variation, weather events and tidal currents, as can the intensity of the pycnocline (i.e. gradient of change in density; Cairns and LaFond, 1966; Skov and Durinck, 2000; Ropert-Coudert et al., 2009a; Kokubun et al., 2010). As the pycnocline approaches tidal-mixing fronts at the boundaries of coastal mixing waters, its depth shallows (Pingree, 1975). Around offshore banks, reduced depths are observed with internal wave passage and localised upwelling (Stevick et al., 2008; Embling et al., 2012).
Sub-surface productivity	May occur over a large area exceeding 10's km's (Weston et al., 2005), or locally in concentrated patches of 100's m's to km's (Scott et al., 2010). Productivity is generally vertically concentrated within a few m's of the pycnocline (Sharples et al., 2001).	Can occur across the summer season, or ephemerally for a few days/weeks (Richardson and Christoffersen, 1991; Sharples et al., 2001; Sharples, 2008).	Productivity and entrainment may be highest when the water column stabilises, following a period of tidal and wave induced vertical mixing (McManus et al., 2005; Cheriton et al., 2007; Durham et al., 2009). May be particularly elevated around offshore banks where internal waves propagate or there is localised upwelling (Lennert-Cody and Franks, 1999; Richardson et al., 2000; Embling et al., 2012).
Offshore banks & internal waves	Spatially predictable and tied to topographic features generally occurring over 1–10's km^2 (e.g. Jones bank; Palmer et al., 2013).	Appear to be seasonal features linked to thermal stratification between late spring and early Autumn. May function intermittently with specific tidal conditions (Embling et al., 2012, 2013; Palmer et al., 2013)	Closely tied to bathymetric structures. Propagation of internal waves may vary with spring-neap modulation and storms (Embling et al., 2013; Palmer et al., 2013). Those associated with the shelf edge (e.g. within the Humboldt current; Bertrand et al., 2008), may be influenced by changes in upwelling intensity.
Tidal-mixing fronts	Small lateral extent of typically 100's m's to 10's km (Schumacher et al., 1979; Decker and Hunt, 1996; Durazo et al., 1998). Length may exceed 10's km's (e.g. tidal mixing fronts around the Bristish Isles; Fearnhead, 1975; Pingree and Griffiths, 1978; Miller, 2009).	Seasonally occurring from late spring to early autumn (e.g. Fearnhead, 1975; Pingree and Griffiths, 1978; Kachel et al., 2002; Acha et al., 2004).	Locations are coarsely predictable and typically tied to a ratio of total water depth (h) and tidal velocity (u) - h/u^3 (Simpson and Hunter, 1974). Inshore/offshore shifts may occur over scales of 10's km's, in response to changes in current strength with the spring-neap cycle, alongside surface induced mixing during wind events and decreased solar irradiance (Kachel et al., 2002; Nahas et al., 2005; Pisoni et al., 2015), which may follow seasonal patterns (Hill and Simpson, 1989). Small scale variation (100's m's to km's) in the surface signature of a front may occur through the tidal cycle and/or due to prevailing wind conditions (Durazo et al., 1998).

(*continued on next page*)

Table 1 (*continued*)

BIO-PHYSICAL HABITAT FEATURE	SPATIAL EXTENT	TEMPORAL EXTENT	SPATIO-TEMPORAL VARIATION
Channels, headland & island wakes, nearshore reefs & bays	Predictable, topographically tied localised features, occurring over 100's m's to a few km's (Zamon, 2002; Johnston and Read, 2007; Bailey and Thompson, 2010; Jones et al., 2014). Some channels, bays and passes may extend across 10's km's (e.g. Academy Bay, Sea of Okhotsk, and passes between Aleutian Islands; Ladd et al., 2005; Rogachev et al., 2008).	May occur perennially, although only at specific times in the tidal cycle (Zamon, 2003; Johnston and Read, 2007; Bailey and Thompson, 2010; Waggitt et al., 2016a).	Functionality may vary with strength and direction of water currents across diurnal and bi-weekly tidal cycles (Johnston and Read, 2007; Bailey and Thompson, 2010; Jones et al., 2014). Local wind patterns may temporarily intensify surface convergences (e.g. occurrence of Langmuir circulation cells; Goss et al., 1997; Ladd et al., 2005).
ROFI's: estuarine plume & tidal intrusion fronts	May be localised over 100's m's (e.g. Moray Firth fronts; Mendes et al., 2002) or larger encompassing 10's to 100's of km's (e.g. Columbine Estuarine & Mississippi River Plume Front; Govoni et al., 1989; Phillips et al., 2018).	Occur perennially, sometimes periodically with the tidal cycle (Simpson and Nunes, 1981; Mendes et al., 2002; Phillips et al., 2018).	Occurrence may be linked to specific phases of the tidal cycle (e.g. Mendes et al., 2002). Geographical location and strength may vary with tidal cycle and experience spatial variation with spring-neap changes in current strength. Local weather conditions and climate will also impact geographical location, occurrence and strength (e.g. rainfall and wind; Kowalczyk et al., 2015b; Phillips et al., 2018). Productivity blooms may follow such cycles (Cloern, 1991).

dolphin *Stenella attenuata*; Baumgartner, 1997; Waring et al., 2001; Pinedo et al., 2002; Azzellino et al., 2008; Scott and Chivers, 2009). Where the shelf edge is nearer to land (e.g. Skagerrak), shorter ranging breeding species may forage at these features (e.g. little auk *Alle alle*; Skov and Durinck, 1998). Shelf-edge fronts may also be important to non-breeding individuals in the late summer, autumn and winter, when constraints to central land-based breeding locations no longer apply (e.g. Cory's shearwater *Calonectris borealis* and little auk; Haney and McGillivary, 1985a; Brown, 1988).

2.2. Wind-driven upwelling fronts

Along the major eastern boundary currents of western North America (the California current), Peru (the Humboldt current) and west Africa (the Benguela, Canary and Somali currents), strong cross winds in combination with Coriolis forcing and Ekman transport form intense upwelling systems, which sustain some of the highest levels of primary and secondary productivity globally (Longhurst et al., 1995). In other regions, similarly structured upwelling systems may occur (e.g. the southern shelf of Australia and along the eastern boundary of the Labrador Current; Kinsella et al., 1987; Kampf et al., 2004), albeit on a smaller and less impressive spatio-temporal scale.

Along, or immediately inshore of the shelf-edge, upwelling fronts mark where these systems meet on-shelf coastal waters. Strong convergent flows accumulate and retain the phytoplankton biomass and small nekton generated by adjacent upwelling systems (Bjorkstedt et al., 2002), which attracts large numbers of pelagic and forage fish (Ainley et al., 2005; Reese et al., 2011; Watson et al., 2018). Due to the typically narrow extent of adjacent shelves (e.g. western Africa and western America's), upwelling fronts are often proximate to land. As such, the prey aggregating effects of these features are exploited by a diverse range of marine predators (Bourne and Clark, 1984; Forney and Barlow, 1998; Hoefer, 2000; Camphuysen and van der Meer, 2005; Croll et al., 2005; Tynan et al., 2005; Ainley et al., 2009) that includes those individuals constrained to land based colonies or a shoreward distribution (e.g. lactating New Zealand fur seals *Arctocephalus forsteri* and Northern elephant seals *Mirounga angustirostris* alongside numerous breeding seabirds such as Cape gannet *Morus capensis*, common guillemot *Uria aalge*, Humboldt penguin *Spheniscus humboldti*, kelp gull *Larus dominicanus*, Peruvian booby *Sula variegata*, rhinoceros auklet *Cerorhinca monocerata* and a number of phalarope species; Briggs et al., 1984; Croll, 1990; Weichler et al., 2004; Ainley et al., 2005; Crocker et al., 2006; Baylis et al., 2008; Sabarros et al., 2014).

The intensities of upwelling systems and their associated fronts can vary seasonally and/or inter-annually with climatic conditions and wind patterns (Kinsella et al., 1987; Bograd et al., 2009a). This can substantially impact the structuring of surrounding ecosystems with concomitant consequences for marine mammals and seabirds (Schneider and Methven, 1988; Schneider, 1994; McGowan et al., 1998; Abraham and Sydeman, 2004; Wolf et al., 2009; Black et al., 2011; Woodson and Litvin, 2015). For example, in years when decreased upwelling intensity reduces the availability of high quality foraging habitats around frontal zones (e.g. with the El Nino Southern Oscillation; ENSO), breeding seabirds along the west coast of the America's may display signs of reduced body condition (e.g. common guillemots; Croll, 1990), or extend their foraging trips (e.g. Cassin's Auklet *Ptychoramphus aleuticus*, Humboldt penguins and marbled murrelet *Brachyramphus marmoratus*), which may result in reduced reproductive success (Becker and Beissinger, 2003; Hennicke and Culik, 2005; Bertram et al., 2017).

3. The mid-shelf: from the shelf-edge to near-shore coastal waters

The mid-shelf extends from the shelf-edge to near-shore coastal waters (Fig. 1), with topographic depths typically ranging from around 50 m–200 m. In mid-latitude, temperate zones this region stratifies seasonally between late spring and autumn, when increased solar irradiation heats surface waters sufficiently to increase buoyancy levels and overcome tidal and wind-driven mixing (Pingree, 1975; Pingree et al., 1976; Simpson and Sharples, 2012). A two-layer system is formed, characterised by a surface mixed layer of warm, nutrient deficient water and a bottom boundary layer of dense, cold nutrient rich water (Fig. 1). This structuring underlies a number of oceanographic processes that appear important to marine mammals and seabirds, particularly in areas where the spatial extent of the continental on-shelf region is large and tidal ranges considerable (e.g. the Canadian, European, northeast USA continental shelf and the eastern Bering Sea Shelf).

3.1. The annual spring bloom

The development/onset of stratification in the spring drives a significant annual phytoplankton bloom (Pingree et al., 1976; Sambrotto et al., 1986; Sharples et al., 2006). The timing of this bloom varies annually as a result of climatic fluctuations in air temperature/solar irradiation and wind stress (Sharples et al., 2006), which can lead to a temporal mismatch between fish spawning and plankton production (match-mismatch hypothesis; Cushing, 1975). This can have bottom-up impacts at higher trophic levels by influencing fish recruitment (Beaugrand and Kirby, 2010; Sigler et al., 2016) and food availability (Durant et al., 2007), and has been shown to effect the breeding success of a number of seabirds including Atlantic puffin *Fratercula arctica*, black-legged kittiwake *Rissa tridactyla*, common guillemot and rhinoceros auklet off the coast of British Columbia, and across the North and Norwegian Seas (Durant et al., 2006; Scott et al., 2006; Borstad et al., 2011). Such impacts sometimes occur at a lag of 1–2 years to underlying shifts in environmental conditions (Zador et al., 2013). Changes in prey availability have also been linked to spatial variability in the distribution of the spring bloom alongside the oceanographic conditions within which it occurs (Fig. 2, Table 1). For example, across the eastern Bering Sea, in years when the spring bloom occurs in warmer offshore waters (due to earlier sea ice retreat; Hunt and Stabeno, 2002), changes in the abundance, composition, distribution and survival of predominant plankton and juvenile fish species results in shifts in the diets and distributions of several seabird populations across the region (Springer et al., 2007; Renner et al., 2016; Hunt et al., 2018), which can have demographic impacts (Satterthwaite et al., 2012; Zador et al., 2013).

3.2. Vertical interfaces in offshore stratified regions (the pycnocline) and sub-surface productivity

Following the spring bloom, productivity within the mid-shelf region redistributes and is maintained by a number of oceanographic processes (Richardson et al., 2000; Weston et al., 2005). An important feature is the vertical interface between the low nutrient, warm surface mixed layer and the cool, dense, high nutrient bottom boundary layer, where steep vertical gradients in density form a pycnocline, that can alternatively be referred to as the thermocline (when vertical density gradients are temperature driven) or the halocline (when vertical density gradients are driven by changes in salinity). This structure acts as a barrier between surface and bottom boundary waters by inhibiting the vertical transport of nutrients and plankton (Stepputtis et al., 2011). In some instances, the pcynocline may be composed of both a thermocline and halocline. Alternatively, the effects of vertical changes in temperature and salinity can cancel each other out, resulting in no pcynocline. Across shelf-seas, offshore seasonal summer stratification is predominantly thermally driven (with a temperature driven pycnocline; Simpson and Sharples, 2012), although in regions subject to high levels of freshwater input (e.g. the Skagerrak between the North and Baltic Seas; Skov and Durinck, 2000), saline gradients may also be important. The majority of studies investigating interactions between marine predators and the pycnocline have focused on links with temperature delineated thermoclines (e.g. Takahashi et al., 2008; Kokubun et al., 2010; Pelletier et al., 2012; Nordstrom et al., 2013; ven Eeden et al., 2016).

High levels of sub-surface primary productivity often concentrate around the pycnocline, and can account for over 50% of water column productivity (Weston et al., 2005) alongside ~30% of total annual productivity (Richardson and Christoffersen, 1991). This is maintained through the summer months by two sources of episodic mixing events, each of which results in an influx of nutrients from the bottom boundary layer that enhances productivity. First, increased tidal currents during spring tides generate turbulent dissipation (due to friction with the sea bed), that may extend up through the bottom boundary layer temporarily eroding the base of the pycnocline (Sharples, 1999, 2008; Sharples et al., 2001; Allen et al., 2004). Second, wave and wind driven surface mixing (due to changes in wave/wind direction and/or velocity with prevailing weather conditions) may partially break down vertical stratification (Sharples and Tett, 1994; Rippeth et al., 2005; Williams et al., 2013). Shear boundaries (strong vertical gradients in horizontal currents) around the pycnocline may additionally aid in the retention of small organisms such as phytoplankton (Franks, 1995; Durham et al., 2009; Cheriton et al., 2010), whilst a synchronous accumulation of zooplankton (McManus et al., 2005) can result in a propagation of food supply across multiple trophic levels.

Sub-surface productivity at and around the pycnocline has been linked to foraging by a number of marine predators, such as little auk, northern fulmar, northern gannet *Morus bassanus* and grey seal *Halichoerus grypus* (Skov and Durinck, 2000; Scott et al., 2010). In diving species, individuals may repetitively descend to the pycnocline (e.g. African penguin *Spheniscus demersus*, northern fur seal *Callorhinus ursinus*, northern right whale *Eubalaena glacialis*, rhinoceros auklet and thick-billed murre *Uria lomvia*; Baumgartner and Mate, 2003; Matsumoto et al., 2008; Takahashi et al., 2008; Kuhn, 2011; ven Eeden et al., 2016), where peaks in prey density (Hansen et al., 2001; Baumgartner and Mate, 2003) increase foraging efficiency (Pelletier et al., 2012). In years when a pycnocline is absent or highly dispersed, foraging success tends to decrease, with concomitant consequences for seabird breeding success (Ropert-Coudert et al., 2009a). Alternatively, individuals (e.g. thick-billed murres in the southeastern Bering Sea) may expand the range of habitats foraged at (both in terms of horizontal extent and dive depth; Kokubun et al., 2010).

The depth of the pycnocline is also an important determinant of foraging habitat suitability (Hunt et al., 1993; Skov and Durinck, 2000; Nordstrom et al., 2013). Increased light attenuation with depth means productivity around shallower pcynoclines is likely enhanced compared with deeper pcynoclines (Skov and Durinck, 2000). Moreover, for near-surface feeders (e.g. northern fulmar) a shallower pycnocline may make prey available at more accessible depths (Skov and Durinck, 2000), and for those that dive from the surface (e.g. least auklet *Aethia pusilla*), reduce foraging energetic costs (Hunt et al., 1990; Haney, 1991; Skov and Durinck, 2000; Langton et al., 2011). In thermally stratified waters, exothermic prey may redistribute themselves near the surface in an attempt to avoid unfavourable cool bottom boundary waters below the pycnoline (e.g. mackerel *Scomber scombrus*; Grégoire, 2006).

3.3. Internal waves and offshore banks

Internal waves form within stratified regions when tidal currents are interrupted by areas of abrupt, raised and/or uneven topography (Fig. 1; Mann and Lazier, 2006), and commonly occur in proximity to the shelf edge (Bertrand et al., 2014) and around offshore banks (Palmer et al., 2013), reefs and rock pinnacles (Moum and Nash, 2000). Resultant locally induced upwelling causes an oscillation in the pycnocline that can exceed an amplitude of 30 m and approach ~50% of local water depth (Witman et al., 1993; Palmer et al., 2013). Nutrient fluxes across the pycnocline sustain exceptionally high levels of sub-surface productivity (Richardson et al., 2000; Tweddle et al., 2013), whilst the simultaneous creation of a number of convergent (aggregating) and divergent (dispersing) zones (Fig. 1) can alter the horizontal and vertical distributions of plankton and small nekton (Lennert-Cody and Franks, 1999; McManus et al., 2005; Bertrand et al., 2008), forcing large aggregations of prey to the surface (Embling et al., 2013) that are foraged at by a range of marine predators (Moore and Lien, 2007; Stevick et al., 2008; Scott et al., 2013; Bertrand et al., 2014). These features appear to be especially important to those taxa that near-surface feed on plankton and/or forage fish such as black-legged kittiwake, humpback whale *Megaptera novaeangliae* and several species of petrel and shearwater (Haney, 1987; Stevick et al., 2008; Hazen et al., 2009; Embling et al., 2012). The generation of internal

waves is tidally mediated (Pineda et al., 2015), and patterns in the occurrence of surface prey aggregations alongside marine mammal and seabird foraging regularly reflect this (Hazen et al., 2009; Embling et al., 2012). Further complexities in the shape of a topographic structure (e.g. steep-sided crests and mounts) may enhance the density of surface aggregations, by simultaneously concentrating tidal currents and moderating the passage of internal waves, to increase upwelling flows and surface convergence (Stevick et al., 2008).

4. Tidal-mixing fronts

Tidal-mixing fronts mark the transition zones between the seasonally stratifying waters of the mid-shelf and mixing coastal waters (Simpson and Hunter, 1974; Pingree and Griffiths, 1978; Schumacher et al., 1979), and are marked by strong horizontal surface temperature gradients (Miller, 2009). Their positions are dependent upon the ability of tidal currents and wind stress to overcome the buoyant effects of surface heat fluxes and mix the entire water column (Fearnhead, 1975; Franks, 1992a; Acha et al., 2004). This is a function of water column depth, and so the position of a tidal-mixing front can be roughly predicted from the ratio of total water depth (h) to tidal velocity (u) - h/u^3 (the Simpson-Hunter parameter; Simpson and Hunter, 1974; Simpson and Sharples, 2012). Once established, variation in a tidal-mixing front's position occurs (Fig. 2, Table 1), in response to changes in the strength of tidal currents with the spring-neap cycle (Sharples and Simpson, 1996; Simpson and Sharples, 2012), as well as from variation in heat flux and wind-driven mixing (Kachel et al., 2002; Nahas et al., 2005; Pisoni et al., 2015).

Tidal-mixing fronts are often associated with elevated and persistent primary productivity that has the potential to propagate across multiple trophic levels (Coyle and Cooney, 1993; Munk et al., 1995; Gregory Lough and Manning, 2001). Where the pycnocline of stratified offshore waters shallows to meet inshore mixing waters, increased light exposure supplemented with runoff nutrients (of coastal waters) alongside those mixed up from the bottom boundary layer results in productivity levels several orders of magnitude higher than in surrounding waters (Pingree et al., 1975; Simpson et al., 1979; Franks, 1992a). Additional convergent flows (Pingree et al., 1974) may redistribute the horizontal and vertical distributions of weak or passively swimming organisms (e.g. plankton grazers attracted to the high productivity levels of the front; Coyle et al., 1998), resulting in near-surface retention and accumulation (Franks, 1992b; Epstein and Beardsley, 2001).

A diverse range of marine predators forage around tidal-mixing fronts (Haney and McGillivary, 1985b; Begg and Reid, 1997; Goold, 1998; Hunt et al., 1999; Weir and O'Brien, 2000). Associations are particularly prominent in colonial seabirds, and land-based breeding sites are often located in proximity to these features (Hunt, 1997). Large numbers of near-surface feeding planktivores, such as least auklet and short-tailed shearwater *Puffinus tenuirostris*, forage at and around tidal-mixing fronts in concordance with patches of increased zooplankton abundance (Hunt et al., 1996; Jahncke et al., 2005), which are often concentrated near the sea's surface (Harrison et al., 1990; Hunt and Harrison, 1990; Russell et al., 1999). These features may also attract large cetacean species including a number of lunge-feeding rorquals (e.g. blue whale *Balaenoptera musculus*, fin whale *Balaenoptera physalus* and humpback whale; Doniol-Valcroze et al., 2007; Dalla Rosa et al., 2012). Piscivores, such as black-legged kittiwake, common dolphin *Delphinus delphis*, common guillemot, Magellanic penguin *Spheniscus magellanicus* and northern gannet, also frequently forage at tidal-mixing fronts (Kinder et al., 1983; Durazo et al., 1998; Goold, 1998; Boersma et al., 2009; Scales et al., 2014b; Cox et al., 2016, 2017), likely because the aggregating effects of these features on plankton predictably attract high densities of forage and pelagic fish (Hansen et al., 2001; Alemany et al., 2009; Brigolin et al., 2018). Across the southeastern Bering Sea, individuals present at these features have been directly linked to high density patches of fish prey (Decker and Hunt, 1996; Kokubun et al., 2008), where capture rates were increased (Vlietstra et al., 2005). For both piscivores and planktivores, fronts with strong surface flow gradients may be particularly attractive, possibly due to additional aggregative effects on small biomass (Schneider et al., 1987). Reduced productivity at frontal zones alongside geographical shifts in typical locations (in years of abnormal oceanographic conditions; e.g. ENSO events) have been linked to increases in short-tailed shearwater mortality rates (Napp and Hunt, 2001).

5. Near-shore coastal waters and estuaries

On the shoreward side of a tidal-mixing front, shallow depths allow turbulence, generated through friction between tidal currents and the seabed, to extend the entire water column and prevent stratification (Simpson and Sharples, 2012). As such, these regions remain permanently mixed throughout the year. Concentrated patches of primary productivity are generally limited to regions of fresh water influence (ROFIs) around estuarine systems. Other notable areas of interest to marine mammals and seabirds, such as those associated with tidally driven turbulence around topographic structures, likely function by mechanically altering the behaviours and distributions of zooplankton and fish prey, as indicated by periodicity in their use (Zamon, 2002, 2003). Unlike the mid-shelf, where the seasonal development of thermal stratification plays a dominant role in the formation of foraging habitat, features occurring in near-shore coastal waters may persist throughout the year and, in some cases, are targeted perennially by marine predators (Skov and Prins, 2001).

5.1. Channels, headland and island wakes, nearshore reefs and bays

In near-shore coastal regions, marine mammals and seabirds frequently forage within tidally active areas (Nol and Gaskin, 1987; Marubini et al., 2009; Anderwald et al., 2012; Benjamins et al., 2015; Warwick-Evans et al., 2016; Waggitt et al., 2018), resulting in distinct regularities in their distributions and behaviours that coincide with particular tidal phases (Becker et al., 1993; Hunt et al., 1998; Irons, 1998; Isojunno et al., 2012; De Boer et al., 2014; Ijsseldijk et al., 2015). Specifically, areas such as narrow channels, headlands, islands, reefs and bays often function as periodic foraging hotspots, where interactions between strong tidal currents (often exceeding $1.5\,ms^{-1}$) and complex topography create prosperous foraging opportunities for marine predators (Cairns and Schneider, 1990; Coyle et al., 1992; Zamon, 2003; Benjamins et al., 2015; Couperus et al., 2016). In some instances, several of these features may occur in close proximity to one another (Bailey and Thompson, 2010).

5.1.1. Channels and narrow passes

Channels, corridors and narrow passes are typical of estuaries, fjords and island groups. During strong tidal flows, these features may act as bottlenecks creating predictable and exploitable concentrations of zooplankton and fish prey advected from adjacent areas (Zamon, 2001, 2002; Couperus et al., 2016), which are exploited by a number of marine mammals and seabirds (Thompson et al., 1991; Lescrauwaet et al., 2000; Zamon, 2001; Holm and Burger, 2002; Hastie et al., 2004, 2016; Ladd et al., 2005; Bailey and Thompson, 2010). Moreover, rapid currents and turbulence along these passages (Nimmo Smith et al., 1999) may disorientate fish and break down shoal cohesion (Liao, 2007), increasing catchability (Zamon, 2001, 2003; Crook and Davoren, 2014). The fine scale foraging distributions of several piscivorous alcids, cetaceans and pinnipeds (e.g. Atlantic puffin, common guillemot, harbour porpoise *Phocoena phocoena* and harbour seal *Phoca vitulina*) across channels and narrow passes are known to concentrate in central and/or narrow areas where current flows are maximised (Pierpoint, 2008; Hastie et al., 2016; Waggitt et al., 2016a). However, it should be noted that due to the energetics of navigating turbulent flows (Wilson et al., 2001; Heath and Gilchrist, 2010), some individuals

forage around the periphery of these currents where speeds are reduced (Pierpoint, 2008; Wilson et al., 2013; Cole et al., 2018; Lieber et al., 2018), and hydrographic fronts and eddies can form (Lieber et al., 2018). Alternatively, such areas may be avoided completely (Wilson et al., 2001; Embling et al., 2010; Waggitt et al., 2016b).

In some cases, the steep sides of a channel, corridor or narrow pass may additionally provide a barrier suitable for prey herding (Heimlich-Boran, 1988), and cetaceans that employ complex group foraging strategies (Simila and Ugarte, 1993; Fertl and Wilson, 1997; Duffy-Echevarria et al., 2008) are frequently observed at these features (Heimlich-Boran, 1988; Hastie et al., 2004; Bailey and Thompson, 2010). Where the edge of a channel or pass acts as a barrier to tidal currents (e.g. in the presence of shallow banks and/or meanders), resultant upwelling and current circulation can force advected zooplankton, and sometimes small nekton (e.g. forage fish), into dense aggregations (Simard et al., 1986; Lavoie et al., 2000; Davies et al., 2013) that may be driven towards the surface (Simard et al., 2002), making these features additionally attractive to both bulk-feeding baleen whales (Cotté and Simard, 2005) and surface feeding birds (e.g. a number of auklet species alongside Bonaparte's *Larus philadelphia* and Mew *Larus canus* gull; Vermeer et al., 1987; Hunt et al., 1998). In some instances, ephemeral features, known as Langmuir circulation cells, form convergent zones at the sea's surface (over scales of a few metres to a couple of hundred metres; Barstow, 1983). These can further entrain plankton and small nekton (Hamner and Schneider, 1986), which near-surface/surface foraging seabirds (e.g. northern fulmars and prions *Pachyptila spp*) have been observed exploiting (Goss et al., 1997; Ladd et al., 2005). Where fast currents pour down into a channel, or where previous upwelled waters descend (e.g. Hunt et al., 1998), downwelling structures may form (Hunt et al., 1998; Waggitt et al., 2016a). Whilst these features have been linked to the foraging distributions of two benthic/demersal feeders (black guillemot *Cepphus grille* and European shag *Phalacrocorax aristotelis*; Waggitt et al., 2016a) alongside one upper-water column feeder (least auklet; Hunt et al., 1998), the exact mechanisms driving these interactions are unclear, but appear to be site and species specific (Hunt et al., 1998; Waggitt et al., 2017).

5.1.2. Headland and island wakes

When headland and island features interrupt the passage of strong tidal current flows, a leeward wake (or eddy) may form. At the interface with non-wake waters, shear induced hydrographic fronts (Wolanski and Hamner, 1988; Johnston and Read, 2007) may accumulate zooplankton which becomes retained within the calm waters of the wake (Alldredge and Hamner, 1980). In addition, turbulent flows around these structures may disorientate fish prey that use the wake to forage, or seek refuge from adjacent strong tidal currents (Liao, 2007; Robinson et al., 2007; Tarrade et al., 2008). For example, in the Bay of Fundy (Canada), harbour porpoise, fin and minke *Balaenoptera acutorostrata* whale exploit dense patches of euphasiids *Meganyctiphanes norvegica* and herring *Clupea harengus* along the edge of an island wake during flood tides (Johnston et al., 2005a,b; Ingram et al., 2007). Bottlenose dolphins in the Moray Firth (UK) concentrate foraging activity along the surface signatures of hydrographic fronts, that form during specific tidal conditions in proximity to a headland on the edge of a deep, steep-sided channel (Bailey and Thompson, 2010), while across Glacier Bay and Icy Strait in southeastern Alaska, humpback whale distributions are disproportionately distributed within the leeward waters of several headlands (Chenoweth et al., 2011). Where fish actively avoid turbulent flows (Nichol and Somerton, 2002), hydrographic fronts may act as a barrier to their movements, and so some predators (e.g. bottlenose dolphin and killer whale) may use these features for prey herding (Heimlich-Boran, 1988; Benjamins et al., 2015). However, as of yet this has not been directly explored.

5.1.3. Nearshore reefs, banks and ridges

Where current flows run across nearshore topographically complex structures such as reefs, banks and ridges, under specific tidal conditions friction can generate shear instabilities, turbulence and upwelling (Coyle et al., 1992; Jones et al., 2014). Peaks in common guillemot, harbour porpoise, phalaropes and thick-billed murre occurrence, corresponding to the locations and times at which these hydrographic features manifest, likely reflect changes in plankton and fish prey distributions that aid capture (Brown and Gaskin, 1986; Coyle et al., 1992; Skov and Thomsen, 2008; Jones et al., 2014). Further offshore, where tidal currents are less pronounced (but still within boundaries of near-coastal regions), bathymetric features such as reefs and ridges may also act to trap plankton and small biomass during downward migrations, which may be particularly attractive to planktivorous species foraging upon euphausiids, such as short-tailed shearwater (Hunt et al., 1996).

5.1.4. Bays

Where the curvature of a headland or series of small islands results in the formation of a bay, complex tidal circulation patterns (enforced by the curved profile of the bay) may accumulate plankton and small nekton through advection and retention (Gomez-Gutierrez and Robinson, 2006; Rogachev et al., 2008). In bays characterised by the presence of steep topographic barriers and ledges, interactions with these circulation patterns can generate localised upwelling. This can force accumulated biomass into dense surface aggregations, which appear to provide important foraging opportunities for a number of planktivorous species that either surface feed (e.g. black-legged kittiwake and red-necked phalarope *Phalaropus lobatus*; Drew et al., 2013; Thorne and Read, 2013) and/or bulk feed (e.g. bowhead whale *Balaena mysticetus* and North Atlantic right whale; Jiang et al., 2007; Rogachev et al., 2008).

5.2. Regions of freshwater influence (ROFIs): Estuarine plume and tidal intrusion fronts

Within and around estuarine systems, typical circulation patterns, forcing dense water below less dense water, promote the two-layer stratification of outflowing nutrient rich freshwater and intruding saline waters (Simpson and Sharples, 2012). Where this stratification meets coastal mixing waters, high horizontal gradients in salinity and density mark the position of either a tidal intrusion front (dense saline coastal water intruding into the estuary) or a plume front (brackish water discharging out of the estuary; Simpson and Nunes, 1981; Lewis, 1984). Stratification increases stability in the water column, and allows plankton to redistribute and settle at or above the salinity driven pycnocline (halocline) where waters are nutrient rich and light exposure increased. Resultant productivity levels are high (Cloern, 1991), and attract large numbers of zooplankton and forage fish (Govoni et al., 1989; Kingsford and Suthers, 1994; Kaltenberg et al., 2010; Phillips et al., 2017), which may be concentrated at the surface signature of the front due to additional convergent flows (Govoni et al., 1989). A number of piscivores, such as black and red throated diver *Gavia stellata/arctica*, bottlenose dolphin, common guillemot, little penguin, northern fur seal and sooty shearwater *Ardenna grisea*, forage at estuarine plume and tidal intrusion fronts (Skov and Prins, 2001; Mendes et al., 2002; Pelland et al., 2014; Zamon et al., 2014; Kowalczyk et al., 2015a; Phillips et al., 2017). The location, occurrence and strength of these features may be tidally mediated and/or dependent upon local current patterns, rainfall and wind events (Sharples and Simpson, 1993; Kingsford and Suthers, 1994; Choi and Wilkin, 2007; Schlacher et al., 2008). Such variability may further impact the abundance and distribution of zooplankton and forage fish, alongside the behaviours of marine mammals and seabirds that forage at these feature (Mendes et al., 2002; Schlacher et al., 2008; Kowalczyk et al., 2015b; Lin et al., 2015; Phillips et al., 2018). For example, bottlenose dolphin foraging at

a tidal intrusion front in the Moray Firth (UK), did so only during flood tide conditions when the front was most pronounced (Mendes et al., 2002), whilst sooty shearwater and common guillemots have been shown to spatially track the boundary of the Columbia River plume (USA) as it evolves through time (Phillips et al., 2018). In Port Phillip Bay (Australia), little penguin breeding success has been linked to the occurrence and intensity of rainfall events, and subsequent changes in the dynamics of a local estuarine plume front and prey availability (Kowalczyk et al., 2015b).

6. Oceanographic habitats and the facilitation of foraging

It is evident that bio-physical processes strongly influence habitat choice by a diversity of marine mammals and seabirds that feed upon plankton and/or forage and pelagic fish, and across shelf-seas a range of oceanographic features are favoured for foraging. Such associations appear attributable to predictable increases in prey accessibility and availability that stem from changes in the abundance and density, depth distribution, behaviour and/or patch persistence of prey, which together likely facilitate trophic transfer and enhance foraging efficiency (Pelletier et al., 2012; Boyd et al., 2016). For example, notable declines in the reproductive success of some marine predator populations have mirrored a change/reduction in the availability of prey enhancing oceanographic habitats following environmental changes with prevailing climatic and weather conditions (Hennicke and Culik, 2005; Scott et al., 2006; Boersma and Rebstock, 2009; Ropert-Coudert et al., 2009a; Wolf et al., 2009; Borstad et al., 2011). The importance of difference aspects of prey availability (e.g. prey abundance versus depth distribution, versus predictability) will depend upon species specific foraging strategies (e.g surface feeder versus diver, available search time, differences in prey type; Hunt et al., 1999; Langton et al., 2011), alongside individual energetic requirements (Hennicke and Culik, 2005; Goldbogen et al., 2011). For central placed foragers constrained to land (e.g. many breeding seabirds and seals), some features may be inaccessible due to their proximity and limitations on an individuals foraging range (e.g. shelf-edge fronts; Thaxter et al., 2012).

6.1. Increased abundance and density of prey

Sites where prey are abundant in dense aggregations allow individuals to reduce foraging effort while maintaining sufficient yields (Enstipp et al., 2007; Benoit-Bird et al., 2013; Goldbogen et al., 2015; Thaxter et al., 2016). Behavioural changes alongside increases in prey capture rates at a number of oceanographic features (Vlietstra et al., 2005; Rogachev et al., 2008; Cox et al., 2016) reflect the presence of abundant and densely concentrated prey (Decker and Hunt, 1996; Vlietstra et al., 2005; Stevick et al., 2008), suggesting these habitats can aid individuals in maximising foraging efficiency (Ropert-Coudert et al., 2009a; Goldbogen et al., 2011; Pelletier et al., 2012). This typically occurs in tandem with increases in primary and secondary productivity (e.g. around shelf-edge fronts, upwelling fronts and tidal-mixing fronts; Decker and Hunt, 1996; Ainley et al., 2005; Jahncke et al., 2005) or specific flow characteristics (e.g. convergent zones at offshore banks subject to the passage of internal waves; Embling et al., 2012, 2013), and may be particularly important for those individuals with especially high energetic needs (e.g. chick provisioning seabirds; Hennicke and Culik, 2005) and/or whose foraging strategies are particularly costly (Green et al., 2009; Goldbogen et al., 2011).

6.2. Depth distribution of prey

Depth distribution plays a key role in prey accessibility, particularly for those taxa that feed at or near the surface and/or have limited dive capabilities (Embling et al., 2012; Boyd et al., 2015). Surface convergent zones at shelf-edge fronts, upwelling fronts and tidal-mixing fronts are frequently used by these foragers, as are localised upwelling structures related to interactions between topography and tidal currents (e.g. at offshore banks and around the coast). In such areas, individuals have been directly linked to shallow prey aggregations (Russell et al., 1999; Stevick et al., 2008; Embling et al., 2012). For diving animals, changes in the depth distributions of their prey may reduce the energetic costs of capture by either allowing individuals to concentrate search activity within a restricted proportion of the water column, or reducing overall dive depths from the surface (Ropert-Coudert et al., 2009b; Benoit-Bird et al., 2011). For example, the foraging efficiencies of some diving seabirds appear to be tied to the presence of vertical prey aggregating features such as the pycnocline (Ropert-Coudert et al., 2009a; Pelletier et al., 2012).

6.3. Prey behaviour

Bio-physical conditions and processes may elicit a change in prey behaviour that further alters densities and depth distributions to increase vulnerability to predation by marine mammals and seabirds. The breakdown of fish school cohesion likely makes individual prey items easier to catch (Crook and Davoren, 2014; Kilian et al., 2015; Hastie et al., 2016), as may the formation of prey concentrations in areas of reduced current speeds (e.g. around island wakes) as fish attempt to avoid such disruptions (Liao, 2007; Robinson et al., 2007; Benjamins et al., 2015). Alternatively, the temperature preferences of some prey mean they may redistribute themselves to aggregate in warmer, near surface waters (Grégoire, 2006).

6.4. Persistence and predictability

The oceanographic features favoured for foraging by marine mammals and seabirds typically occur in a persistent and/or predictable manner. If individuals can learn and remember the locations at which encountering accessible prey is more probable (Hunt et al., 1999; Gende and Sigler, 2006; Weimerskirch, 2007; Davoren, 2013; Regular et al., 2013; Grecian et al., 2018), concentrated search effort (Hamer et al., 2009; Pettex et al., 2010; Dragon et al., 2012; Patrick et al., 2014) can increase foraging efficiency (Stephens and Krebs, 1986). Targeted search patterns have been shown to coincide with the occurrence of a number of oceanographic habitats that are repetitively visited (Bailey and Thompson, 2010; Sabarros et al., 2014; Scales et al., 2014b). Moreover, these behaviours have been shown to develop as individuals mature, suggesting they are beneficial (Grecian et al., 2018). In some cases, the scales across which targeted search effort occur are tied to those of corresponding physical processes. For example, gannets foraging around tidal-mixing fronts restrict search behaviours over scales of between 2 km and 10 km (Hamer et al., 2009; Scales et al., 2014b), reflective of those over which the locations of these features vary with tidal- and wind-driven events (Nahas et al., 2005; Pisoni et al., 2015). Bottlenose dolphins foraging around topographically controlled tidal structures display highly localised search behaviours over 100's of metres, which mirrors the similarly scaled predictability of these features (Bailey and Thompson, 2010).

7. Future research directions

Whilst associations between marine predators and bio-physical processes have been documented across numerous studies, there are a number of areas in which improvements are still necessary. Concurrent measurements of sub-surface oceanography, low-to mid-trophic level prey distributions and marine mammal and seabird behaviours around many discrete physical features are lacking (e.g. tidal stream environments), or limited to a specific set of locations and sites (e.g. the Bering Sea, British Isles and Canadian Continental Shelf). Moreover, fine-scale three-dimensional measurements of marine mammal and seabird movements are rarely integrated, which would allow for estimates of prey capture attempts and energetic expenditure to be calculated and

used to evaluate foraging effort/efficiency (Viviant et al., 2010; Watanabe and Takahashi, 2013; Richard et al., 2016). Achieving this would greatly increase our understanding of how physical habitats impact prey availability for marine predators and facilitate trophic transfer (Embling et al., 2012), whilst also elucidating site and species specificity (Waggitt et al., 2017) alongside the drivers of spatio-temporal variability in marine mammal and seabird distributions (Certain et al., 2007). Such efforts may also elucidate the importance of other, lesser studied structures. For example, to our knowledge, the ecological significance of bottom fronts (which may be important to deeper diving predators) is yet to be investigated (Hill et al., 2008). In addition, despite some evidence suggesting Langmuir circulation cells may be exploited by surface feeding seabirds in near-coastal regions (Goss et al., 1997; Ladd et al., 2005), the importance of these features further offshore is yet to be explored (Barstow, 1983). Distinguishing the way in which individuals perceive their environment via knowledge transfer (Machovsky-Capuska et al., 2014), learning and memory (Regular et al., 2013; Grecian et al., 2018), sight (Bodey et al., 2014; Tremblay et al., 2014; Bairos-Novak et al., 2015) and smell (Savoca and Nevitt, 2014) would also be beneficial, as would an increased knowledge of immature/juvenile foraging behaviours and how these develop through time (De Grissac et al., 2017; Votier et al., 2017; Grecian et al., 2018). Further inter-taxa research (e.g. marine mammals versus seabirds, planktivores versus piscivores, and surface feeders versus divers) would compliment this, and provide additional insight of the selection pressures that have shaped the evolution of the at-sea behaviours of these animals, and driven the necessary adaptations required for foraging in dynamic waters. Such investigations may also be useful for assessing the importance of multi-species feeding associations (Camphuysen and Webb, 1999; Veit and Harrison, 2017), alongside the potential of different taxa to adapt in response to climate change. Finally, there is a distinct lack of studies determining the importance of oceanographic habitat features at a population level, which should be addressed. Future research should aim to fill these gaps if we are to improve our understanding of habitat use by marine mammals and seabirds across shelf-seas. However, achieving this will require novel methodological techniques. Adaptive survey designs (e.g. Embling et al., 2012; Suberg et al., 2014; Waggitt et al., 2014, 2016a; Benjamins et al., 2016; 2017) that incorporate active and passive acoustics (Williamson et al., 2015, 2016; Benoit-Bird and Lawson, 2016; Macaulay et al., 2017; Lieber et al., 2018; Malinka et al., 2018) alongside underwater videography (Machovsky-Capuska et al., 2011; Crook and Davoren, 2014) may prove particularly useful, as will animal-borne biologging via the attachment of accelerometers (Viviant et al., 2010; Watanabe and Takahashi, 2013; Chimienti et al., 2016), cameras (Votier et al., 2013; Watanabe and Takahashi, 2013; Tremblay et al., 2014), GPS loggers (Yoda et al., 2014), oceanographic sensors (Charrassin et al., 2008) and satellite relay systems (e.g. the Argos satellite system; Photopoulou et al., 2015; CLS, 2016; Cox et al., 2018). Moreover, outputs from remote-sensing and oceanographic modelling can be used to initially identify discrete features of interest (Scales et al., 2014a; Waggitt et al., 2016a), and/or provide data over extended areas/time-spans/retrospectively. This may require novel processing and analytical routines, that can characterise and link bio-physical processes to information on animal behaviour and movement (e.g. d'Ovidio et al., 2004; Miller, 2009; Embling et al., 2012; Boyd et al., 2014; Bayle et al., 2015; Lieber et al., 2018; Mattei et al., 2018; McClintock and Michelot, 2018; Pirotta et al., 2018), with particular attention paid towards the spatio-temporal scales of investigations (Fig. 2, Table 1; Mannocci et al., 2017; Scales et al., 2017). Ideally, multiple approaches should be combined and integrated with demographic data, which would yield an overview of ecosystem dynamics unprecedented in detail (Boyd et al., 2015; Barbraud et al., 2017; Carroll et al., 2017), and can later be used to force individual and population based models to determine the adaptability of these environments to future change (e.g. anthropogenic or climatically driven; Boyd et al., 2016; Barbraud et al., 2017).

8. Applications to conservation management

Over the last 20–30 years, marine management and policy has started to evolve from single species based protocols and strategies (typically tailored to a specific fishery/sector), to more holistic methods that consider ecosystems in their entirety, and incorporate more precautionary conservation measures (e.g. the European Marine Strategy Framework Directive, 2008/56/EC; Pikitch et al., 2004; Arkema et al., 2006; Curtin and Prellezo, 2010). Key to this is the preservation of core shelf-sea habitats, such as those oceanographic features identified here as favourable for foraging by marine mammals and seabirds (Hooker and Gerber, 2004; Taylor et al., 2005; Heithaus et al., 2008; Game et al., 2009; Dickey-Collas et al., 2017; Sherley et al., 2017). However, achieving adequate protection is complicated by the diverse nature of such structures, which occur over a range of spatio-temporal scales (Fig. 2 and Table 1), and function via a variety of bio-physical mechanisms that may impact prey availability in different ways (e.g. through inducing changes in depth distribution, persistent, predictability, abundance and/or behaviour; see section 6). A sophisticated understanding of these dynamics should be used to effectively implement appropriate and customised conservation management strategies (Wilson, 2016; Authier et al., 2017).

For example, initial implementations of holistic management have focused on fixed area based protection through the designation of marine protected areas (MPAs; Hyrenbach, 2000; Hooker and Gerber, 2004). Here, the aim is to reduce overlap with spatially explicit threats (e.g. commercial fisheries, marine renewables and maritime traffic) that may cause direct mortality and/or disrupt accessibility to favoured habitats (e.g. through prey depletion or displacement; Pichegru et al., 2010; Gormley et al., 2012). However, while persistent and predictable bathymetrically tied tidal features (e.g. offshore banks, channels and island wakes) may be particularly well suited to such measures, to accommodate individuals relying on habitats that are variable through space and time (e.g. upwelling and tidal-mixing fronts), adaptive approaches are required. A recent solution to this is dynamic ocean management (DOM), defined as management that is adjustable through space and time in response to the shifting nature of the ocean and its users (Hobday et al., 2014; Lewison et al., 2015; Maxwell et al., 2015). Such methods can thus allow for geographical changes in habitat locations with, for example, prevailing environmental conditions (e.g. position in spring-neap cycle alongside short term weather events, seasonal trends and longer term climatic changes; Nahas et al., 2005; Bograd et al., 2009a; Pisoni et al., 2015). However, implementing DOM requires multidisciplinary and novel monitoring approaches, so as boundaries are effectively designated and modified (Hazen et al., 2018). Moreover, attention needs to be paid towards the spatio-temporal scales over which data is acquired and protection implemented, which should reflect the characteristics and spatio-temporal variability of an oceanographic feature (Fig. 2, Table 1; Mannocci et al., 2017; Scales et al., 2017). Satellite remote-sensing can aid in this by allowing oceanographic features to be tracked both instantaneously in near real time and over longer periods, although this is only applicable where a distinct surface signature is presented (Miller, 2009; Scales et al., 2014a). Sensors deployed on diving animals, autonomous/unmanned survey vehicles and/or moorings may compliment such information (Charrassin et al., 2008; Suberg et al., 2014; Photopoulou et al., 2015), as can outputs from oceanographic and statistical modelling (Brodie et al., 2018; Mattei et al., 2018). Where stationary management is preferred, long-term time series data may be used to develop buffer zones that extend the boundaries of a fixed MPA, such that fluctuations in the spatio-temporal occurrence of a habitat feature is captured (e.g. the entire spring-neap/weather dependent range of a tidal-mixing front; Nahas et al., 2005; Grantham et al., 2011; Pisoni et al., 2015). Such strategies should still be evaluated at regular intervals to assess potential geographical shifts in response to climate change (Queiros et al., 2016).

A shift towards management strategies than consider habitat hydrology in addition to geography is also beneficial to ensuring that the functioning of oceanographic features favoured for foraging is maintained (Dickey-Collas et al., 2017). For example, anthropogenically generated structural changes to the marine environment (e.g. marine renewable energy installations; MREIs) may alter the bio-physical and spatio-temporal characteristics of oceanographic environments (e.g. interruptions to near coastal current regimes may alter and/or manifest tidally driven features such as hydrographic fronts, wakes and localised upwelling systems; Brostrom, 2008; Shields et al., 2011; Benjamins et al., 2015; Fraser et al., 2018). This may cause shifts in the geographical locations at which these structures occur and impact prey availability (e.g. depth distribution and predictability; Becker and Beissinger, 2003), and thus should be carefully considered during the planning stages of development projects. Impact assessments at sites where oceanographic features favoured for foraging are present need to consider how variability in the dynamics of such structures influence patterns in area use by marine mammals and seabirds, and thus the validity of associated evaluations (Benjamins et al., 2017; Cox et al., 2017). Climate change impacts will likely also alter the functioning of these habitats. Increases in the frequency and intensity of extreme climatic (e.g. ENSO associated changes in upwelling; Cai et al., 2014) and weather (e.g. storm induced turbulent mixing; Young et al., 2011) events may again, modify the dynamics and geographical locations of critical oceanographic features (Hazen et al., 2013; Sherley et al., 2017), such as upwelling fronts, the pycnocline and tidal-mixing fronts (Ropert-Coudert et al., 2009a; Pisoni et al., 2015). For example, decreases in the reproductive outputs of a number of seabirds have been linked to changes in the availability of oceanographically generated foraging habitats following irregularities in prevailing climatic and weather conditions (Hennicke and Culik, 2005; Durant et al., 2006; Scott et al., 2006; Ropert-Coudert et al., 2009a). Minimising the impacts of this will require adaptive, innovative and precautionary management strategies that minimise cumulative stressors (Field and Francis, 2006; Lester et al., 2010; Sherley et al., 2017), particularly since our understanding of how ecosystems will cope and respond to such alterations is largely unknown. Again, MPAs and DOM informed by studies on the dynamics of oceanographic features favoured for foraging will likely play an important role in this (Halpern et al., 2010; Grantham et al., 2011; Briscoe et al., 2016; Dickey-Collas et al., 2017).

9. Conclusions

A range of oceanographic features are favoured for foraging by marine mammals and seabirds across shelf-seas in mid-latitude temperate zones. Whilst associations are diverse and variable in nature (both between sites and across species), in the majority of cases intricate interactions between bathymetry and tidal currents play a dominant role, alongside patterns in seasonal stratification and shelf-edge upwelling. The attractiveness of a favoured oceanographic feature appears to stem from persistent and/or predictable increases in prey accessibility which facilitates foraging. Changes in prey abundance, density, behaviour and depth distribution are fundamental to this, and in a number of cases have been shown to improve foraging efficiencies. However, our knowledge of interactions between marine predators and oceanographic features favoured for foraging is far from complete, and future work should aim to further our understanding of the functional mechanisms linking bio-physical processes, prey and marine mammals and seabirds. In many instances, detailed and simultaneous three-dimensional measurements of sub-surface oceanography, prey densities and distributions alongside marine predator behaviours (also across three dimensions) are lacking, and this should be addressed. Such efforts may also elucidate the importance of lesser studied features such as bottom fronts and Langmuir circulation cells. A better understanding of how predators perceive their environment and develop foraging strategies during immature/juvenile stages would also be beneficial, as would comparative inter-taxa research and estimates of the importance of oceanographic habitat features at a population level. Knowledge of the bio-physical processes that underlie habitat use by marine mammals and seabirds across shelf-seas should be used to inform future conservation management and policy. This will require improvements in the monitoring of oceanographic conditions such that adaptive strategies can be implemented which, where necessary, can evolve through space and time in response to spatio-temporal variability. This would aid the preservation and protection of shelf-sea oceanographic features that facilitate trophic transfer, and are thus critical to the functioning of shelf-sea environments. Such holistic approaches are vital to ensuring the future health of these complex ecosystems.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.ecss.2018.06.022.

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